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Changes in Compensatory Eye Movements Associated with Simulated Stimulus Conditions of Spaceflight

DEBORAH L. HARM, M.S., Ph.D., LINDA M. ZOGRAFOS, B.A., M.S., NOEL C. SKINNER, B.S., M.S., and DONALD E. PARKER, B.A., Ph.D.

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Compensatory vertical eye movement gain (CVEMG) was recorded during pitch oscillation in darkness before, during and immediately after exposures to the stimulus rearrangement produced by the Preflight Adaptation Trainer (PAT) Tilt-Translation Device (TTD). The TTD is designed to elicit adaptive responses that are similar to those observed in microgravity-adapted astronauts. The data from Experiment 1 yielded a statistically significant CVEMG decrease following 15 min of exposure to a stimulus rearrangement condition where the phase angle between subject pitch tilt and visual scene translation was 270°; statistically significant gain decreases were not observed following exposures either to a condition where the phase angle between subject pitch and scene translation was 90° or to a no-stimulus-rearrangement condition. Experiment 2 replicated the 270°-phase condition from Experiment 1 and extended the exposure duration from 30 to 45 min. Statistically significant additional changes in CVEMG associated with the increased exposure duration were not observed. The adaptation time constant estimated from the combined data from Experiments 1 and 2 was 29 min.

IN 1983, WE OBSERVED a phenomenon that was not anticipated either by us or by our astronaut observers: head roll in darkness within 1–2 h after a Space Shuttle landing elicited perceived self motion that included a strong translational component (10). Later observations, which included voluntary head roll both during entry and immediately after landing, replicated this

basic finding (14). The perception of translation was not universal and was often complex. Specifically, the astronaut may attribute the motion to him/herself, to the visual surround, or to both. Nevertheless, this observation suggested that something had changed during microgravity, a change that was somehow associated with the way in which signals from graviceptors were interpreted. This basic finding, as well as several follow-up observations, led to the proposal of an otolith tilt-translation reinterpretation (OTTR) hypothesis to account partially for astronauts' sensorimotor adaptation to microgravity.

The OTTR hypothesis is based on "otolith ambiguity." Otolith receptors are stimulated both by accelerated translational motion and by tilt with respect to gravity. Due to the equivalence of linear acceleration and gravity noted by Einstein, graviceptors, including otolith receptors, are unable to distinguish tilt with respect to gravity from accelerated translational motion (6). Possible mechanisms for resolving "otolith ambiguity" include the following: (a) neural integration of otolith, semicircular canal, and visual signals; and (b) temporal filtering so that long time-constant signals are interpreted as tilt while short time-constant signals are interpreted as translation. The observations from returning astronauts suggest that adaptation to microgravity includes resetting of the neural integrator and/or time constants to favor the translation interpretation.

MATERIALS AND METHODS

Simulation of Microgravity with a Tilt-Translation Device

Based on the OTTR hypothesis, we designed an apparatus to accomplish a similar "resetting" process on Earth (8,10). As illustrated in Fig. 1, the TTD couples translational movement of a visual scene with respect to an observer with tilt of both the observer and the visual surround. The TTD simulates microgravity in only a

From the Space Biomedical Research Institute, NASA-Johnson Space Center, Houston, TX (D. L. Harm, L. M. Zografos, N. C. Skinner) and the Spatial Orientation Research Laboratory, Department of Psychology, Miami University, Oxford, OH (D. E. Parker).

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Address reprint requests to: Deborah L. Harm, Ph.D., who is a Research Psychologist, NASA-Johnson Space Center, Mail Code SD5, Houston, TX 77058.

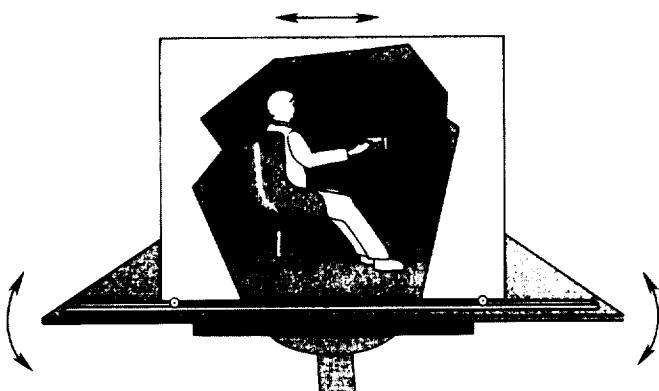


Fig. 1. The Tilt-Translation Device is a one degree-of-freedom tilting platform on which are mounted a visual surround (enclosed box) and a subject restraint. The visual surround moves linearly parallel to the subject's X body axis. Both the visual surround and the subject are oscillated in pitch. See text for details.

restricted way. Specifically, it decouples semicircular canal and otolith signals from visual signals; further, visual and otolith signals are combined in a manner intended to bias the interpretation of the otolith signals as translation.

The rationale for the TTD is as follows. In microgravity, otolith stimulation results from translational acceleration and tangential shear associated with off-axis rotation. In the TTD, otolith stimulation, achieved by tilt with respect to gravity in pitch or roll, is coupled with translational motion of the visual surround. Investigators who study responses to stimulus rearrangements, such as those produced by prisms and mirrors, report that an observer's perceived movement and orientation is determined principally by the visual stimulus. This phenomenon has been labelled "visual capture" (16). To the extent that an observer's perception of self-motion in the TTD is determined by the visual scene motion, the signal from the otolith receptors should be biased toward the translation interpretation and this bias should also be reflected by eye movement changes.

The TTD does not simulate the tangential shear associated with off-axis rotation. Although the TTD simulation of microgravity is very limited, it is designed to elicit the same state that has been observed in microgravity-adapted astronauts following their return to Earth.

Previous Research with the Tilt-Translation Device

Previous experiments using a prototype TTD revealed that compensatory vertical eye movement gain (CVEMG) was reduced following exposure to the stimulus rearrangement (SR) produced by that device (9). Also, subjects reported less perceived tilt and greater translation during pitch stimulation in darkness following the exposure than prior to it.

Other experiments with the prototype trainer were conducted to examine the effects of roll stimulation on horizontal eye movements and self-motion perception (11,12). Results similar to those of the pitch oscillation studies were reported. However, quite variable re-

sponses were obtained with the TTD prototype due to the lack of precise stimulus control and the relatively crude eye movement analysis procedures. Therefore, an apparatus capable of enhanced stimulus control was constructed. We postulated that stimulus parameters (profiles) which would produce more consistent evidence for adaptation could be identified.

Using the new TTD that controls phase relationships between head/body tilt and visual surround translation, Reschke et al. (15) examined the effects of several SR profiles on translational self-motion perception. They reported that perception of self-translation was greatest when the platform tilt/visual surround translation phase relationship was 270° and least when this phase relationship was 90° (Fig. 2).

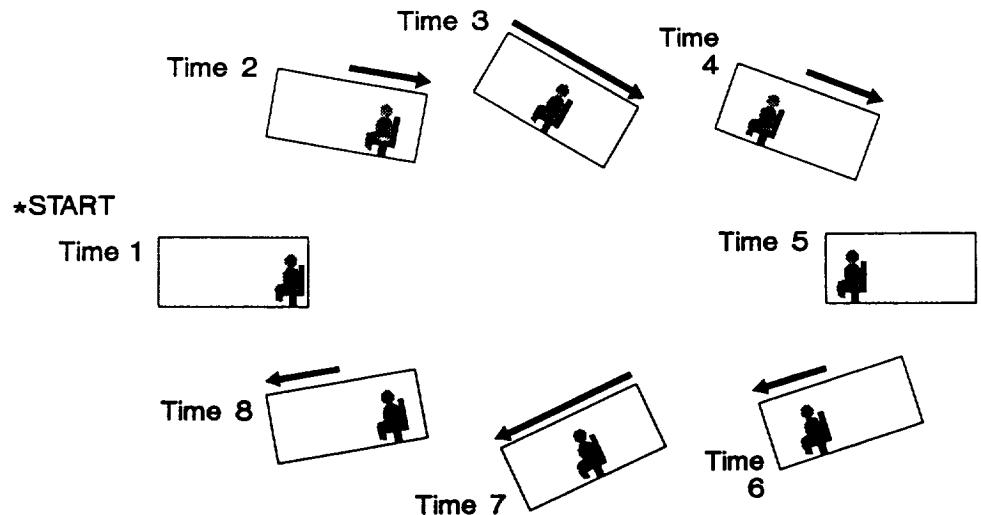
Hypothesis that 270° Phase Angle is Optimal for Adaptation

We hypothesized that exposure to the 270° phase condition would result in decreased CVEMG for the following reasons. First, in the "pitch configuration" the TTD is designed to facilitate the forward-rearward (X axis) translational self-motion interpretation of otolith and somatosensory graviceptor cues and to suppress the pitch self-motion interpretation. Second, if the subject interprets graviceptor cues as indicating translation, vertical compensatory eye movements should be reduced. Third, adaptation should be greatest when the visual motion cues and graviceptor cues combine to support a translation interpretation. This combination is greatest for the 270° phase condition because the responses evoked by visual surround motion direction and velocity are congruent with graviceptor responses evoked by the force changes associated with pitch position and direction.

The rationale for expecting that the 270° phase condition would result in adaptation follows (Fig. 2). First, perceived forward self-motion translation is elicited by rearward motion of the visual surround. Perceived forward self-motion should be greatest when the visual surround velocity is greatest. Second, forward self-motion translation is elicited by increased pressure on the subject's back and lower buttock as well as by rearward (occipital) displacement of the otoconia. The force acting on the vestibular otolith organs and the skin pressure stimulation varies with pitch position. At time 3 in Fig. 2, the forward translational self-motion perception evoked by the peak velocity visual surround movement toward the subject is congruent with the skin pressure cues from the subject's back and the occipital otoconia displacement evoked by the maximum backward pitch position. At this time, the otolith and skin pressure cues are similar to those that would be elicited during real forward translation. Similarly at time 7, the graviceptor cues evoked by forward pitch are congruent with the visually-induced rearward self-motion evoked by the visual surround peak velocity.

Based on the preceding analysis, it is also reasonable to expect that a 90° phase condition would result in less translational self-motion perception than the 270° condition. As noted above, in the 270° phase condition, skin pressure and otolith cues are congruent with visual sur-

Fig. 2. Position of subject relative to visual-surround position and velocity for the 270° phase stimulus rearrangement condition (SR-270). At time 1, the visual surround is at its most forward position and is stationary with respect to the subject; the subject is upright. At time 2, the surround has moved rearward relative to the subject and both the subject and the surround are pitched backward. As indicated by the arrow above the box, the surround reaches 71% of its peak velocity at this time. At time 3, the visual surround reaches peak velocity and the subject is in the most backward pitch position. At time 4, the subject and surround are returning to upright and the surround velocity is reduced. Finally, at time 5, the subject is upright and the surround is stationary. Forward translation of the surround with respect to the subject and forward pitch of both the surround and the subject occurs from time 6 to time 1.



round motion. This is not the case for the 90° condition; rather, otolith and skin pressure cues similar to those that would be elicited during real forward translation are coupled with visual scene motion that indicates rearward translation of the subject. If cue incongruence leads to less translational self-motion perception in the 90° condition, as reported by Reschke et al. (15), a smaller decrease of CVEMG would be expected for this condition than for the 270° condition.

EXPERIMENT 1

The purpose of Experiment 1 was to replicate and extend previous observations (9,11,12,15) using the new TTD. We predicted that CVEMG would decrease following exposure to a 270° phase profile (SR-270) and that no CVEMG change would be observed following exposure to a 90° profile (SR-90) or a No-SR condition (pitch tilt in darkness).

Method

Subjects: Fourteen subjects (ages 20 to 37 years) who were naive with respect to the motion capabilities of the TTD and the hypotheses being tested were recruited from the NASA-Johnson Space Center subject pool. Each had passed an Air Force Class III physical exam within 1 year prior to participation in the study and none reported a history of inner ear or vision deficiencies.

Apparatus: The TTD is a one degree-of-freedom tilting platform on which the subject is restrained in a car seat (Fig. 1). In the pitch configuration and with the head restrained, the axis of tilt rotation is approximately aligned with the subject's interaural axis. A box mounted on the platform moves linearly parallel to the subject's X body axis to provide a translating visual stimulus. The visual surround is a 76 × 35 × 36-in (193 × 88 × 91-cm) white box with vertical black stripes on the side walls and horizontal stripes on the ceiling. The stripes are 2.25 in (5.7 cm) wide and 0.5 in (1.27 cm) thick and are separated by 3.25 in (8.25 cm). Four successively smaller outlined black squares and a solid

black square in the center are attached to the inside of the end wall facing the subject. The line width and separation between lines is progressively smaller from the outer to the inner square to produce the appearance of a tunnel. Visual surround illumination is provided by four 7.5-W red lamps attached to the ceiling behind the subject.

Hydraulic motors drive both the tilting platform and the visual surround. The amplitude, frequency and phase angle between platform and visual surround oscillation are under computer control.

Procedures: Upon arrival at the laboratory, subjects were provided with a brief description of the experimental protocol and completed an informed consent form. Electrodes for electro-oculographic (EOG) measurement were then applied above and below the right eye and a reference electrode was placed behind one ear. Subjects were then fitted with red-lensed goggles which were worn for 20 min prior to, as well as during, the experiment to stabilize the corneo-retinal potential. The goggles permit a 160° field of view.

The following stimulus parameters were used in Experiment 1 for the SR-270 condition: exposure duration, 30 min; platform and visual surround oscillation frequency, 0.1 Hz; pitch tilt amplitude, ±4°; visual surround translation amplitude, ±15 in (38 cm); phase relationship between platform pitch and visual surround translation, 270° (Fig. 2). For the SR-90 condition, all of the stimulus parameters were the same except that the phase relationship between platform pitch and visual surround translation was 90°. For the No-SR condition the subject, who was in darkness, was oscillated in pitch at the same frequency and amplitude as used for the two SR conditions. The low frequency of pitch oscillation was chosen to minimize semicircular canal contributions to the CVEMG (see Discussion).

Vertical eye movements and subject pitch angle position data were sampled at 120 Hz and stored on a disk for later analysis.

Each subject was exposed to the three stimulus profiles (SR-270, SR-90, and No-SR) on different days sep-

arated by a minimum of 1 week. Order of exposure to the three profiles was randomized across subjects. Subjects were led blindfolded and seated in the apparatus; they were not allowed to see any part of the apparatus except the interior of the surround during the SR profiles. During exposures, subjects were instructed to keep their heads stationary and their eyes open, but they were not required to fixate on any specific point within the surround. A black foam-core collar was positioned on the subjects' shoulders to prevent viewing of the floor and the moving platform. Finally, a padded Velcro® strap was used to restrain the head against the chair headrest. During the No-SR exposure, subjects were pitched in complete darkness and were instructed to keep their eyes open. Frequent conversation between the subject and test operator maintained subject alertness.

The vertical EOG was calibrated prior to each 2-min data-collection run by instructing the subject to fixate a stationary light-emitting diode while the chair was oscillated in pitch at $\pm 8^\circ$. During data collection trials, which were conducted in total darkness, the subjects were instructed to fixate an imagined target at the same distance as the target used during calibration. Data were collected before and at 15 and 30 min during exposure to each of the stimulus conditions.

Motion sickness symptoms were monitored throughout the exposure session. If a subject accumulated more than 7 symptom points on the Pensacola Motion Sickness Scale (7), the exposure was terminated, and the EOG data were excluded from further analysis.

Results

Complete EOG data were obtained from 10 subjects. The other four were dropped from the study because their responses failed to meet the criteria described below. All of the subjects spontaneously reported perceived self-translation during the SR exposures. The strength of perceived self-translation varied across subjects and generally became stronger during the exposure.

EOG analysis: EOG data were selected and analyzed following a procedure described elsewhere (3). Gaze fixation on an imaginary, stationary target during passive sinusoidal head motion is a difficult task. Due to variability in subject attention, electronic noise and other factors, EOG records varied. Consequently, the experimenter decided which records were to be included in the analysis. In general, EOG records selected for analysis were characterized by smooth, symmetric sinusoids where the peak-to-peak amplitude was constant from cycle to cycle and the signal variability was approximately constant. Data were excluded from the analysis if there was evidence of eye blinks; large saccadic eye movements apparently of voluntary origin; EOG signal drift characterized by a gradual rise or fall of the record; advanced or delayed peaks perhaps associated with saccadic, voluntary tracking; saccadic peak clipping/overshoot; or electrode/amplifier noise. Data were selected principally from the zero-crossing region of the eye position signal. This corresponds to the time of peak slow-phase velocity; the trace was most regular during this interval.

EOG data reduction was accomplished with an interactive program. Segments of the data that did not meet the criteria specified above were removed by computer-assisted manual editing of the EOG records. The remaining slow-phase eye movement amplitudes were fitted to sine functions in order to obtain a gain value for each trial. Vertical eye movement gain was defined as vertical eye movement amplitude divided by head pitch amplitude. Raw EOG data from one subject before and after exposure to the SR-270 condition are illustrated in Fig. 3.

Statistical analysis: Eye movement gain values were analyzed using a two-way (conditions by time) repeated-measures analysis of variance. The predicted conditions-by-time interaction illustrated in Fig. 4-A was significant [$F(4,34) = 4.62$; $p < 0.005$]. The simple main effect of time was significant for the SR-270 condition [$F(2,18) = 10.42$; $p < 0.001$]. *Post hoc* testing (Tukey) indicated that CVEMG was greater before exposure than at 15 or 30 min after the beginning of exposure; the gain values at 15 and 30 min after exposure were not significantly different. The simple main effects of time for the SR-90 and No-SR conditions were not significant: the mean gain values across time were not significantly different for those exposure conditions. This analysis and Fig. 4 indicate that the greatest reduc-

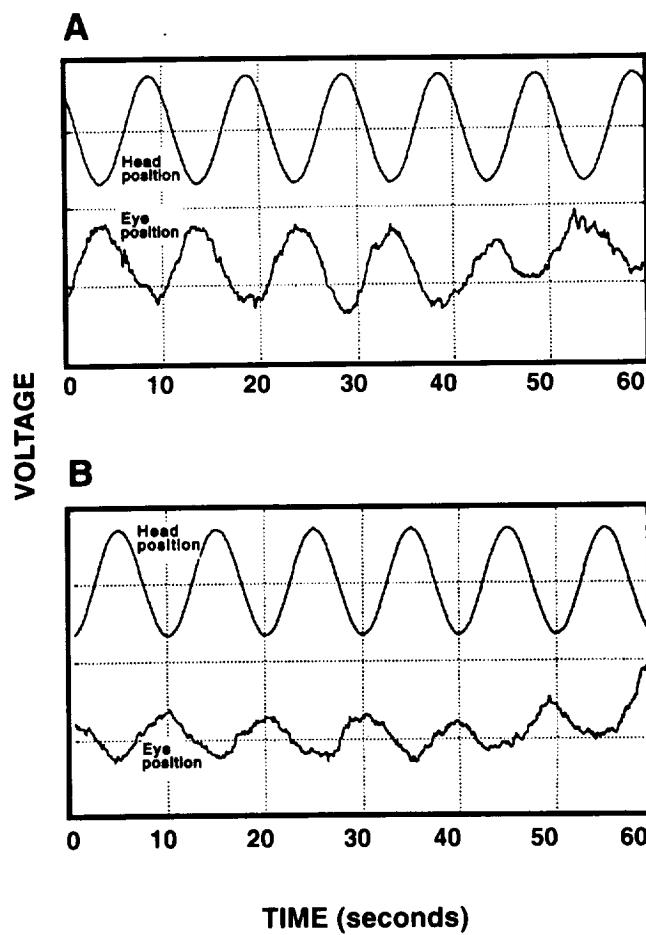


Fig. 3. Compensatory vertical eye movements recorded while the subject fixated an imagined stationary target during 8° pitch oscillation at 0.1 Hz (A) before and (B) after 30 min exposure to the 270% stimulus rearrangement condition.

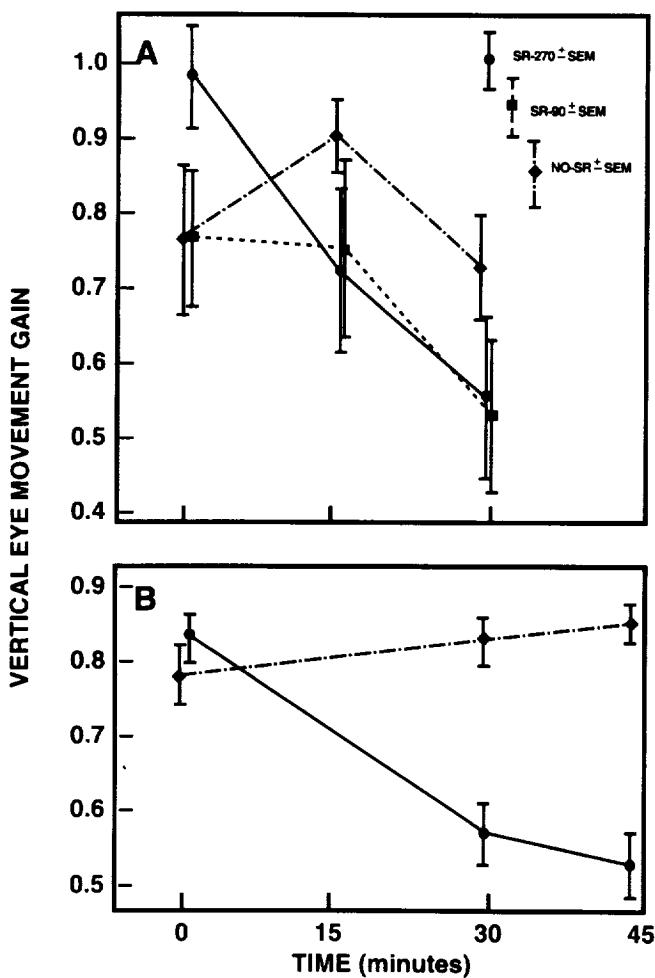


Fig. 4. Compensatory vertical eye movement gain as a function of time of testing. Fig. 4-A: Mean gain values from Experiment 1 prior to exposure, after 15 min of exposure, and after 30 min of exposure to three stimulus profiles. The curves suggest that eye movement gain was decreased following exposure to the 270° stimulus rearrangement and was unchanged following exposure to the 90° stimulus rearrangement and no-rearrangement conditions. For the 270° condition, the major decrement in gain occurred during the initial 15 min of exposure. Fig. 4-B: Mean gain values as a function of time of testing (pre-exposure, after 30 min of exposure, and after 45 min of exposure) recorded in Experiment 2. The results suggest that exposure to the stimulus rearrangement for durations greater than 30 min did not increase the amount of adaptation.

tion of CVEMG occurred following the initial 15 min of exposure to the SR-270 condition.

While the results of the statistical analysis support the hypothesis, it should be noted that the curves in Fig. 4-A exhibit an unexplained difference at baseline: the gain for the SR-270 data set is larger than for the SR-90 and No-SR data sets prior to the onset of SR exposure. This baseline difference may contribute to the observed differences across the three stimulus rearrangement conditions.

EXPERIMENT 2

The purposes of the second experiment were three-fold: first, to replicate the findings of Experiment 1 regarding the SR-270 condition; second, to determine the degree to which extending the duration of the exposure

period to 45 min would modify the decrease in CVEMG beyond that obtained following a 30-min exposure; and third, to determine whether interrupting the exposure to the SR after 15 min for EOG data collection affected the overall CVEMG reduction obtained at 30 min.

Methods

Thirteen new subjects (ages 20 to 40 years) recruited from the same subject pool as those in Experiment 1 participated in Experiment 2. The apparatus and procedures were identical to those used in Experiment 1 with three exceptions. First, the total duration of exposure to the conditions was 45 min. Second, EOG data were collected after 30 min of continuous exposure to a motion profile and again after an additional 15-min exposure. Third, the SR-90 condition was not included.

Results

Seven subjects completed the second experiment. Six were dropped because their EOG records failed to meet the criteria described previously. As in Experiment 1, all of the subjects spontaneously reported perceived self-translation during the SR exposures.

EOG data reduction procedures were the same as for Experiment 1. CVEMG values were analyzed using a two-way (conditions by time) repeated-measures analysis of variance. As in Experiment 1, the predicted conditions-by-time interaction illustrated in Fig. 4-B was significant [$F(2,11) = 22.16$; $p < 0.0001$]. Analysis of the simple main effects for the SR-270 condition indicated a significant effect of time [$F(2,12) = 26.63$; $p < 0.0001$]. Post hoc testing indicated that the pre-exposure gain was greater than the postexposure gain at both 30 and 45 min; the gain values 30 and 45 min postexposure were not significantly different. The simple main effect of time was not statistically significant for the No-SR condition.

DISCUSSION

Basic Observations

The reduction of eye movement gain following the SR-270 exposure suggests that subjects adapted to the stimulus rearrangement produced by the TTD. Statistically significant changes in CVEMG were not observed following the SR-90 or No-SR exposures. Overall, the results from Experiments 1 and 2 replicate the observations reported previously (9,11,12) that CVEMG is decreased following exposure to the TTD.

The curve in Fig. 4-A for the SR-90 condition does suggest that exposures for periods greater than 30 min may elicit adaptation in the form of CVEMG reduction. Perhaps the phenomenon of visual capture, described above, may be sufficient to overcome incongruence between visual, otolith, and somatosensory cues. Specifically, exposure to a stimulus rearrangement that includes visual stimulation may result in adaptive responses even where the inertial stimulus is incongruent with that visual stimulus. Support for this possibility derives from the work of Khater and his colleagues (5) which demonstrated that a horizontal semicircular canal signal can drive vertical eye movements.

The second major observation from these experi-

ments was that the largest change in eye movement gain was observed following the initial 15 min of TTD exposure. Increasing exposure duration to 30 min or 45 min did not result in statistically significant further gain reduction. The observation of rapid adaptation reported above is consistent with reports by Khater et al. (5) that the adaptation time constant for vertical vestibuloocular reflex (VOR) gain changes following exposure to a "VOR direction adaptation procedure" was 36 min. The data for the SR-270 conditions from Experiments 1 and 2 were combined and the adaptation time constant was estimated to be 29 min. Similar rapid adaptation to the stimulus rearrangement produced by magnifying lenses was reported by Collewijn et al. (1).

The variability in the data for Experiment 2 was less than one-half of that for Experiment 1. This reduction may be attributed to several factors including better subject selection, improved communication between the subject and the experimenter, and increased skill by the experimenter in using the interactive eye movement analysis program.

Relationship between TTD Stimulus and Microgravity

An investigation of astronauts' self-motion and self-orientation reports in microgravity immediately after landing and in the TTD has recently been completed and is being prepared for publication. These reports suggest that the TTD may elicit self-motion illusions that are similar to those experienced during entry. After several minutes in the apparatus, one astronaut stated that "I feel as though if I pushed on the wall I would float across the room." This and similar reports suggest that the TTD effectively re-invoked that astronaut's neural program for microgravity. This leads to the suggestion that the TTD simulates microgravity in the sense that it may alter neural processing of signals from spatial orientation and motion receptors in the same way that microgravity alters that neural processing.

Comment Regarding Visual Stimulus—Graviceptor Stimulus Match

For the TTD stimulus profiles used in this investigation, 15-in (38-cm) visual surround displacement was combined with a 4° platform pitch. At first glance, this may appear to result in a mismatch in the physical stimuli. However, we suggest that that mismatch does not present a serious difficulty for the following reasons. The visual stimulus is made ambiguous deliberately. As noted above, the end wall facing the subject contains successively smaller rectangles to simulate a tunnel. This visual stimulus distance ambiguity was designed to allow the subject to "scale" perceived distance to the walls so that the expanding and contracting looming pattern and optic flow would match the simulated physical acceleration stimulus (see reference 13). Also, the visual surround translation is intended to elicit illusory perceived translational self-motion. Results from other studies suggest that the relationship between visual surround motion and perceived self-motion is not tightly bound (2,4). As above, the subject may well be able to scale the visual stimulus to match the stimulus from physical tilt.

Potential Limitations

Semicircular canal stimulus produced by TTD: As noted previously, a low frequency of oscillation was chosen to minimize semicircular canal contributions to the CVEMG. Undoubtedly the stimulus that we used was in the range that stimulates the canals. However, the 4° (half sine) pitch is small relative to the commonly experienced 90° pitch movement associated with transition from lying supine to standing. Given the 0.1 Hz oscillation frequency, this canal stimulus is near threshold for many subjects. In contrast, the stimulus to the otolith and somatosensory receptors (assuming that shear is the effective stimulus and the equivalence of gravity and physical linear acceleration) was equivalent to a linear acceleration of about 68 cm/s². Clearly, a 4° pitch provides a strong stimulus to the graviceptors. Also, as noted previously, astronauts report perceived translation elicited by head roll during entry and immediately after landing. Our hypothesis, which is congruent with that adopted by other investigators, is that otolith and other graviceptor signals are responsible for this phenomenon. These observations lead us to suggest that the adaptation exhibited by the subjects in these experiments was due primarily to the altered relationship between visual and graviceptor stimuli.

Potential contribution of motion sickness and drowsiness to CVEMG reduction: We suggest that the results of these experiments were due to adaptation rather than to motion sickness or drowsiness for the following reasons. As noted above, none of the data included in this study were from subjects who were motion sick, as defined by the accumulation of more than 7 points on a motion sickness scale. Drowsiness was reduced by using an alerting procedure to maintain attention during the adaptation phase of the trials, which were themselves somewhat arousing. The eye-movement recording tests were relatively brief, associated with an alternation in the stimulation environment (which is arousing) and accompanied by conversation between the experimenter and the subject. These factors are inconsistent with the explanation that the observed CVEMG reduction was due to motion sickness or drowsiness.

Conclusions

The results of this investigation are consistent with the view that astronauts can be pre-adapted to one aspect of the microgravity of spaceflight by learning a specific new relationship between otolith graviceptor and visual motion signals. The data suggest that 15- to 30-min exposures to a SR-270 condition should be adequate to elicit appropriate adaptive changes.

The major benefit of exposure to the stimulus rearrangement produced by the TTD may be to decouple visual and inertial signals. By permitting astronauts to experience environments where visual and inertial self-motion signal relationships differ from those ordinarily experienced on Earth, the astronauts may be better prepared to cope with the stimulus rearrangement that they encounter in microgravity. To the extent that decoupling is an appropriate goal, the specific phase relation-

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ships between the inertial and visual stimuli may not be very important.

Research is currently being pursued to determine the effects of repeated exposures and the maximum time interval across which adaptive changes can be demonstrated. Further information regarding preflight adaptation training rationale, apparatus and procedures is presented by Parker and Parker (9).

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